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BIOLOGY OF EPIPHYLL FEEDING BUTTERFLIES IN A NIGERIAN COLA FOREST (LYCAENIDAE: LIPTENINAE)

Curtis J. Callaghan
Avenida Suba 130-25 Casa 6, Bogota, Colombia

ABSTRACT. I describe the adult behavior of 16 liptenine butterfly species (Lycaenidae) and include descriptions of oviposition behavior and immatures of 12 from a cola forest near Lagos, Nigeria. Larvae of all species fed on epiphylls such as lichens and fungi, and adults fed at extrafloral nectaries on forest bamboos and vines. I conclude that most species have strictly defensive relationships with ants, the butterfly larvae using their long setae and crevasses in the bark for protection. Larvae of one species (*Aethiopana honorius*) inhabit *Crematogaster* ant runs, and avoid ant attacks by a combination of speed and defensive use of their long lateral setae.

Additional key words: Nigeria, defensive behavior, ants, larval behavior.

No studies of Nigerian Lycaenidae have been published since the classic articles by Farquharson (1921) and Lamborn (1913). These and subsequent works by Jackson (1937), dealing with a wider African fauna, considered mainly those liptenine species associated with ants. Of species not associated with ants, some information is available on two *Telipna* species, one *Mimacraea*, one *Liptena* (Jackson 1937), and two *Pentila* (Clark & Dickson 1971). Here, I report the biology of 12 additional species of Lipteninae, of which 11 are not associated with ants. Notes on adult behavior are included for 16 species. I conclude with a discussion of adult and larval habits.

Study Area and Methods

I observed and collected lycaenid butterflies over a two-year period near Lagos, Nigeria. The study area (Fig. 1) was a small forest on the edge of a swamp near Agbara, an industrial estate 40 km west of Lagos. The dominant tree species was *Cola nitida* (Vent.) Schott & Endl., which grows to a height of 10–15 m, forming a closed canopy. Most primary forest in the region has been destroyed, but cola trees are preserved because of the commercial value of their red, pink, and white nuts, which are used locally for chewing and ceremonial purposes. Even so, the cola forest is threatened by the demand for firewood and living space by the nearby urban population. In this surviving cola forest the understory vegetation is usually left to grow along with a few cacao and banana trees that are not sprayed, thus forming a good habitat for many forest species.

I made observations on liptenine biology from July 1986 to March 1988. During the second year I made trips to the study area nearly every weekend, weather permitting, spending a total of 29 days in the field. Initially, I started observations at 0900 h and terminated them at

1600 h. After four months of such long hours, I limited my field time to between 1000 and 1530 h, which I had discovered to include the peak of lycaenid activity. Field observations were recorded on a portable tape recorder and later transcribed to a notebook.

I collected eggs in two ways: by following ovipositing females in the field and by inducing females to lay eggs in captivity. Following females proved unsatisfactory because it required searching the substrata for eggs with a hand lens, by which time the female had usually gone, making identification uncertain. By confining field caught females in plastic bags or wide mouth jars with a piece of moist lichen-covered wood inside, some species could be induced to oviposit. The containers with the females were kept in a naturally ventilated room with no direct light. After hatching, larvae were transferred to jars with fresh epiphyll-covered wood and closed with tissue paper to allow ventilation and prevent mold. High humidity prevented use of totally closed containers, which quickly became moldy, with consequent ill effects for the eggs and larvae.

SPECIES ACCOUNTS

The following 16 liptenine species were recorded at the study site and are listed with observations on their habits and biology.

Ptelina carnuta (Hewitson, 1873)

On numerous occasions I observed adults, both male and female, feeding during the morning hours at extrafloral nectaries of vine tendrils and bamboo, as many as four together and often in the company of other liptenines and ants. When landing, *P. carnuta* held their wings vertically after flexing them a few times.

One female oviposited 5 orange eggs singly on leaf litter on the forest floor at about 1530 h. The female and eggs were taken to the lab, but the eggs never hatched and the female would not oviposit in captivity. Two subsequent attempts to induce other females to oviposit in plastic bags in which dried leaves had been placed also failed.

Pentila nigeriana Stempffer and Bennett, 1961

Adults of both sexes fed on tendril and bamboo nectar between 1000 and 1200 h. Males perched around the trunks of prominent trees on the edge of small openings in the forest between 1100 and 1330 h, which they would circle with a slow, fluttering flight about 4–5 m off the ground before coming to rest on a nearby dry branch. When alighting, they flexed their wings a few times before resting with the wings folded over their backs.

FIGS. 1–6. **1,** Cola forest habitat, Agbara, Lagos, Nigeria. The taller trees are *Cola nitida*; **2,** *Pentila bitje* ovipositing on a dead branch; **3,** *Liptena opaca* feeding on extrafloral nectaries of a creeper; **4,** Third instar larva of *Larinopoda aspidos* feeding on epiphylls; **5,** Male *Aethiopana honorius* resting on bamboo stem; **6,** Larva of *A. honorius*. Note long lateral setae.

A single female oviposited on dried branches near the forest floor at 1340 h. The eggs were laid singly. Brought into the lab, she later placed many reddish-brown eggs on a lichen covered stick in a plastic bag, but the eggs never hatched.

Pentila picena cydaria (Grose-Smith, 1898)

Pentila picena was an avid feeder at bamboo nectaries, with up to 6 individuals of both sexes feeding on the same stem. Male perching habits were similar to *P. nigeriana*, with which *P. picena* shares perching trees. Like *P. nigeriana*, adults of *P. picena* used the tree trunks as reference points, landing on nearby dried branches from which they flew if disturbed, making a few slow circles around the trunk before alighting on the same branch as before and flexing their wings a few times.

I made nine observations of females of this species ovipositing in the forest between 1320 and 1500 h. Eggs were laid singly on live trees and woody stems covered with green lichens and moss. When laid, eggs were white, then became dark brown within a day. In one case two eggs were placed near one another on the same trunk. One female brought into the lab laid numerous eggs on the inside of a glass jar. None of the eggs, either field collected or obtained in the lab, hatched.

Pentila bitje Druce, 1910

The males of this species perched in the company of those of *P. picena* and *P. nigeriana* around the same tree trunk. Flight was slow and fluttery. They alighted invariably on dried branches or tendrils, flexing their wings 3–4 times before closing them over their backs. I observed both sexes feeding on tendril and bamboo extrafloral nectar during the morning (1000 to 1230 h).

On six occasions I observed females ovipositing dark brown eggs (Fig. 2) on dead twigs and branches covered with epiphylls and located near the ground and abandoned termite mounds. Eggs were laid singly between 1300 and 1500 h. Three times I induced females to oviposit in the lab. The larvae hatched in twelve days, refused to eat and died two days later. First instar larvae were light brown with setae longer than the body and extending dorsad and cephalad.

Telipna rothi (Grose-Smith, 1898)

Both sexes fed throughout the morning on bamboo extrafloral nectar. They spent the rest of the day resting in the deeper forest on the undersides of low branches with wings folded. When disturbed, their flight was fairly rapid, similar to that of *Acraea bonasia* Cramer, from which they are indistinguishable on the wing. Upon landing, they did

not flex their wings, their cryptic undersides blending into the background.

One female brought in from the field oviposited brown-gray eggs on dead lichen-covered sticks placed in a plastic bag. The eggs hatched after 10–11 days and the larvae fed on the lichens, spending much of their time in the crevasses or under loose bark. They molted to second instar 9 days later, but refused to eat, despite the introduction of new lichens, and died. Eggs laid by a second female failed to hatch. The head of the second instar was black, thorax and abdomen gray-green with dark lines between the segments, and covered with long setae, the longest dorsad.

Ornipholidotos kirbyi (Aurivillius, 1895)

This species congregated in numbers of up to 6 individuals of both sexes in the morning on vine tendrils and the tips of bamboo shoots where they fed at extrafloral nectaries in the company of ants. When approached by ants, they lowered their wings, keeping them in that position until the ants had retreated. Between 1230 and 1430 h males perched on branches 5–7 m below the forest canopy in groups of up to 4 individuals. Here they chased each other in circles, then landed on branches, and did not flex their wings. Inducing females to oviposit in captivity was unsuccessful.

Mimeresia libentina libentina (Hewitson, [1866])

Both sexes fed between 0900 and 1200 h on bamboo and tendril extrafloral nectaries. Between 1200 and 1500 h males rested just inside the edge of the woods, hanging from tendrils or dried branches less than 2 m above the ground. Upon landing, they flexed their wings for a minute or two before closing them.

Eresiomera cornesi (Stempffer, 1969)

I observed both sexes feeding on bamboo extrafloral nectaries in the morning. Females appeared to be rare, only two being captured during the two year study period. Between 1200 and 1430 h, males were common at their perching site, which was a large tree trunk around which they chased each other in circles, never lower than 4 m above the ground. To rest, they landed on the tree trunk, flexing their wings a few times.

Citrinophila marginalis Kirby, 1887

Between 0900 and 1600 h, males congregated around the trunks of certain trees, where they rested on nearby leaves 3 to 5 m above the ground. They returned to the same perch after being disturbed, flexing

their wings a few times. Only once did I observe this species feeding on bamboo nectar.

On five occasions I saw females ovipositing in the late afternoon (1400–1500 h). Flying slowly through the undergrowth, females landed on live, smooth-barked trees as well as on dead twigs, upon which they deposited a tiny dark brown egg. Ovipositing females did not flex their wings. Twice females in the lab laid eggs, both times on the sides of the container rather than on the lichen-covered sticks provided. Seven days later the transparent, pubescent larvae hatched, started feeding on the lichen material, and gradually turned the same color as the lichens. However, after the second day of feeding, all larvae stopped eating and died.

Citrinophila erastus erastus (Hewitson, [1866])

Males perched high in the upper story of the forest just below the canopy, 6–7 m above the ground, between 1100 and 1340 h. They rested for long periods on leaf surfaces, flying only when disturbed. Like *C. marginalis*, they flexed their wings a few times upon landing. Lone females were encountered only twice, moving slowly through the undergrowth near the ground in the early afternoon.

Liptena similis (Kirby, 1890)

This species fed on bamboo extrafloral nectaries during the morning (900–1230 h). They congregated in groups of 4–5 individuals of both sexes on a shoot, driving ants away by lowering their wings.

In the laboratory one female oviposited tiny, dark brown eggs with nearly smooth shells. The pubescent brown larvae hatched 13 days later, but refused to eat and died.

Liptena opaca opaca (Kirby, 1890)

In the morning (900–1200 h) this species fed in groups at the nectaries of forest creepers and bamboo shoots in the company of ants and other liptenines (Fig. 3). They lowered their wings to drive away ants. Males chased one another high in the canopy and remained on the wing for long periods, circling in a small area without landing.

I saw one female oviposit on dry branches near the forest floor during the afternoon, but later, in the laboratory, she did not continue ovipositing.

Larinopoda aspidos Druce, 1890

Groups of 5 to 6 individuals of both sexes fed on tendril and bamboo extrafloral nectaries during the morning. Males did not appear to have specific perching sites, but flew in wide, low circles in open areas in

the forest. Adults did not flex their wings when landing, although they lowered their wings to push ants away when feeding. Males have a slightly faster flight than *Pentila*. Females, when searching for oviposition sites, resembled a small white pierid, *Leptosia*, which is very common in the same woods.

I observed 13 ovipositions on dead, epiphyll-covered branches in the woods between 1300 and 1600 h. Females also oviposited readily in the lab. The dark brown eggs hatched within 10 days and the pubescent first instar larvae fed on lichens, seeming to prefer a pale green variety. Molt to the second instar occurred 7 to 9 days later. Individual larvae varied in development time, some molting 3–4 days ahead of their siblings. Second and third instars (Fig. 4) had dark bands on the thoracic and abdominal segments and, on both thorax and abdomen, setae which curve up from the sides and over the back, ending with white bulbous tips, similar to the larvae of *Liptena undina* Smith and Kirby described by Jackson (1937). Molt to the third instar occurred 7 to 10 days later. Larvae crawled under loose pieces of bark, avoiding direct light. They fed almost continuously except the 2 days before molt. Later instars fed on rotten wood as well as on lichen. No larvae survived the third instar.

Tetrarhanis diversa (Bethune-Baker, 1904)

I observed both sexes of this tiny butterfly in the company of other liptenines feeding at tendril and bamboo extrafloral nectaries in the deep forest during the morning.

Twice I found females ovipositing on dead, lichen-covered sticks on the forest floor around 1300 h. After placing a single egg, the female would fly 10 to 20 m before depositing another egg on another stick. None of the three eggs brought into the lab hatched.

Epitola dunia Kirby, 1887

The conspicuous blue males perched during the late morning and early afternoon on the edge of large, sunlit clearings, flying rapidly along the forest margins, then returning to their original perches. They usually rested on dried branches 2–4 m above the ground, their cryptic undersides making them difficult to spot. They did not flex their wings. Females primarily remained deeper in the forest, appearing on the forest margins for mating, where I discovered a copulating pair at 1100 h. I observed one individual of this species being chased and caught by a bird.

I saw a female ovipositing on a dead palm frond at 1315 h. The disk shaped egg hatched 9 days later, but the pubescent larva refused to eat and died after 2 days. Although this genus is reported to be associated

with ants (Lamborn 1913, Jackson 1937), there were no ants where the oviposition was observed.

Aethiopana honorius (Fabricius, 1793)

Males perched in late morning (1100 to 1300 h) on the edge of small sunlit clearings, where half a dozen or more were found together, and not far from the ant trees utilized by their larvae. Males rested by hanging from dead branches or from the bamboo stems from which they fed (Fig. 5). Females frequent the same clearings, but more rarely. Normal flight was rapid and high, the males spectacular as they flashed among the trees. When disturbed while perching, they flew only a short distance before alighting. Their underwing pattern mimics that of distasteful *Bematistes* (Acraeinae).

One female brought into the lab laid a single, disc-shaped egg with serrated edges which did not hatch. Females flew around trees infested with *Crematogaster* ants (Formicidae) and I discovered two larvae moving about the ant runs on the tree trunk near the ant's carton nests. The larvae were dark reddish brown with long lateral setae, and with the body tapering caudad (Fig. 6). Although they normally did not pay attention to the larvae, the *Crematogaster* ants became very aggressive when aroused, as I discovered when I was removing an *A. honorius* larva from the tree. The ants attacked it and were able to get between the setae, causing wounds from which it later died. The second larva was brought into the lab where it fed on lichens for three weeks before dying.

DISCUSSION

Adult Behavior

Liptenine adult behavior is summarized in Table 1. Perching activity by males revealed no marked habitat partitioning in time and space by congeneric species as has been recorded for Neotropical Riodinidae (Callaghan 1983). Most congeneric liptenine species perched in the same localities and over long periods. Perching for most species occurred from slightly before noon until 1400 h, only *C. marginalis* perching earlier in the morning (at 0900 h). Five of 13 species consistently perched near trees, but only one (*cornesi*) actually rested on the tree. Most species landed on dry branches or creepers. In the field, liptenines can be differentiated from butterflies of other families that they mimic, such as Acraeidae, by their resting substrate and behavior. Only the two *Citrinophila* species rested on flat leaves.

Wing flexing upon landing was found only in *Ptelina, Mimeresia, Pentila, Eresiomera,* and *Citrinophila,* all of which share a character-

TABLE 1. Summary of liptenine behavior.

Species	Perching			Wingflex[4]	Ovipositing	
	Site[1]	Time[2]	Sub-strate[3]		Substrate[5]	Time
P. carnuta	—	—	C	Y	A	1530
P. nigeriana	A	11–1330	A	Y	B	1340
P. picena	A	11–1400	A	Y	C	1320–1500
P. bitje	A	12–1400	A	Y	B	1300–1500
T. rothi	—	—	A	N	B	—
O. kirbyi	B	13–1430	A	N	—	—
M. libentina	C	1030–1400	A	Y	—	—
E. cornesi	A	12–1430	C	Y	—	—
C. marginalis	A	900–1600	B	Y	B, C	14–1500
C. erastus	B	11–1340	B	Y	—	—
L. similis	C	11–1400	A	N	—	—
L. opaca	B	12–1400	A	N	B	1400
L. aspidos	C	11–1300	A	N	B	13–1600
T. diversa	—	—	A	N	B	1300
E. dunia	C	10–1300	A	N	B	1315
A. honorius	C	11–1300	A	N	—	—

[1] Perching Site: A = around a perching tree; B = high above ground, just below canopy; C = woods edge or large sunlit clearings.
[2] Perching Time indicates the hours of the day during which perching was observed.
[3] Perching Substrate: A = tendrils and dry branches; B = leaves; C = tree trunk. For species not observed perching, the substrate used for normal resting is given.
[4] Wingflex refers to the pumping movement of the wings while the butterfly is at rest: Y = yes; N = no.
[5] Oviposition Substrate: A = leaf litter; B = dried branches; C = live branches or tree trunks.
[6] Dash = not observed.

istic slow flight. This behavior may be an advertisement of distastefulness. Despite their slow flight, I never saw birds take any interest in them, although I once observed an *E. cornesi* being stalked by a small lizard. Although the lizard made several attempts to reach the resting butterfly, it was unable to catch it.

Oviposition took place between 1200 and 1600 h for all species observed. Females placed eggs primarily on dry, epiphyll-covered branches near the forest floor, except for *Pentila picena*, which utilized live epiphyll-covered substrates, and *Citrinophila marginalis* and *Larinopoda aspidos*, which used both. *Ptelina carnuta* oviposited on dry leaf litter. All eggs in nature were laid singly and widely spaced, with the exception of one observation of *P. picena*, in which 2 eggs were placed on the same tree trunk.

The major food resource for adult liptenine butterflies was the nectar from extrafloral nectaries. Some forest creepers and bamboos produce from their growing tips a sweet nectar that attracts ants and liptenine butterflies. From morning to early afternoon some creeper and bamboo stems may be visited by numbers of liptenines of different species, which appear not unlike small flags on a pole (Fig. 3). To keep ants away, the butterflies lower their wings and maintain them in that position until the ants have moved away. Whether or not this behavior

has the effect of releasing ant repellant pheromones as suggested by Atsatt (1981) could not be determined.

In wing pattern, *Citrinophila*, *Larinopoda*, and *Liptena* species mimic Pieridae; *Telipna* and *Aethiopana* resemble Acraeinae; and *Telipna* mimic day flying moths.

Behavior of Immatures

Once thought to be rare, the use of epiphylls (liverworts, lichens, bacteria, algae, and fungi) as larval foodplants by butterflies appears to be widespread. Evidence presented here, in addition to that in Jackson (1937), Fahrquharson (1921), and Clark and Dickson (1971), suggests that this is a major larval food resource for the lycaenid subfamily Lipteninae, currently with 46 genera. In addition, two Satryinae (Singer et al. 1971, DeVries 1986) and one Neotropical genus of Riodinidae, *Sarota* (DeVries 1988, Callaghan unpublished), have been recorded feeding on these food sources. The list probably will grow with future research.

All observations on liptenine larvae were made in the lab from eggs found in the forest and from females induced to oviposit in plastic bags or jars. In the latter case females laid as many as 50 eggs on the sides of the containers or on wood placed inside. However, as all field observations suggested that eggs are laid singly, the number of eggs laid in the lab was presumably a result of the confined environment and stress. Many times the eggs did not hatch, for reasons unknown. In only two cases did larvae pass the first instar and in no case did larvae produce adults. My observations suggest that larval diet is varied, both lichens and rotten wood (fungus?) being consumed by the same species. The food resource of *A. honorius* is the black varnish (fungi/feces?) left by the ants along their runs (Farquharson 1921), although they will feed on epiphylls as well.

One of the major determinants of larval behavior and morphology is their relationship with ants. Among the liptinines I observed, this relationship took two forms; purely defensive, in which the larvae merely protected themselves from aggressive ant behavior (the majority of the species) and opportunistic, in which the larvae took advantage of the ant's aggressiveness for protection against other predators (only in the case of *Aethiopana honorius*).

Cola forests are invaded periodically by driver ants, especially during the rains. Driver ants advance quickly and viciously on a wide front, attacking any creature in their path irrespective of size. Insects and other small animals are immobilized and dismembered in minutes. To test the driver ants' reaction to Lepidoptera larvae, I placed several unidentified pierid larvae among the ants, which immediately attacked

and killed them. The sluggish lichen feeding liptenine larvae would likewise be easy prey, lacking the thick cuticle and ant appeasing nectar glands found in other lycaenids (Atsatt 1981, Cottrell 1984). Also, there is no evidence that liptenines produce pheromones that appease or repel ants. The principal protection for liptenine larvae appears to be their long setae. Once, I observed small red house ants (genus undetermined) enter the *L. aspidos* larva jar and take up residence in the wood. Normally quite aggressive, the ants left the larvae alone after encountering the setae. As larvae spend much time in the crevasses in the bark, the setae apparently form a protective umbrella that prevents ants from getting close enough to bite them. The use of long setae for protection against ants has been suggested by Jackson (1937), Cottrell (1984), and DeVries (1988).

Other liptenine larvae seek protection among ants while not providing any direct benefit to them, such as honeydew secretion. Genera with this behavior are *Aethiopana*, *Hewitsonia*, *Tetatoneura* (Farquharson 1921, Jackson 1937, my own observations in Zaire) and *Epitola* (Jackson 1937), although in the case of the latter my observation of oviposition far from the ant runs may suggest both purely defensive and opportunistic behavior for that genus.

Aethiopana honorius larvae evidently avoid predation by inhabiting ant runs, which are hostile environments for many potential predators. Other Lepidoptera larvae without long hairs and other insects that I placed in the ant runs were immediately attacked. Although the ants do not normally bother *honorius* larvae, they will attack if excited and will bite the larvae if they can get between or under their setae, as related earlier. Farquharson (1921) described a similar experience in which larvae in a jar were attacked by ants. Larvae of *A. honorius* are protected by their long setae and by moving about the ant runs on their long legs at a speed equal to that of the ants themselves. When the ants become excited, the larvae beat a hasty retreat, flicking the last abdominal segments to shake off any attacking ants that may have become lodged among their setae. Similar behavior occurs among *Hewitsonia* larvae in Zaire (Callaghan unpublished), suggesting an exception to the assertion by Cottrell (1984) and Atsatt (1981) that lycaenid larvae lack a "thrashing reflex" found in other lepidopterous larvae, presumably because rapid movements incite ant aggression. The rapid movement of *A. honorius* and *Hewitsonia* transports them out of danger by not allowing excited ants the chance to gang up on them; the flicking removes ants entangled in the setae. Such behavior also works because the larvae remain in the runs where ants are not densely packed, category L2 of Cottrell (1984). The larvae will not enter the ants' carton nests. I tried pushing a *Hewitsonia* larva towards the nest, but it kept

trying to move in the opposite direction. There is nothing in the behavior of larvae of either species that would suggest that they use ant appeasing pheromones.

Finally, in addition to living in the ant runs, larvae with long setae gain additional protection from vertebrate predation by mimicking larvae of moths of the family Lymantriidae, which also inhabit the same ant runs and have tufts of stinging dorsal spines.

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